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Standing on the Shoulders of Apes: Analyzing the Form and Function of the Hominoid Scapula Using Geometric Morphometrics and Finite Element Analysis

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ABSTRACT

Objective: The aim was to analyze the relationship between scapular form and function in hominoids by using geometric morphometrics (GM) and finite element analysis (FEA).
Methods: FEA was used to analyze the biomechanical performance of different hominoid scapulae by simulating static postural scenarios. GM was used to quantify scapular shape differences and the relationship between form and function was analyzed by applying both multivariate-multiple regressions and phylogenetic generalized least-squares regressions (PGLS).
Results: Although it has been suggested that primate scapular morphology is mainly a product of function rather than phylogeny, our results showed that shape has a significant phylogenetic signal. There was a significant relationship between scapular shape and its biomechanical performance; hence at least part of the scapular shape variation is due to non-phylogenetic factors, probably related to functional demands.
Discussion: This study has shown that a combined approach using GM and FEA was able to cast some light regarding the functional and phylogenetic contributions in hominoid scapular morphology, thus contributing to a better insight of the association between scapular form and function. Am J Phys Anthropol 159:325–341, 2016. © 2015 Wiley Periodicals, Inc.

Primates live in diverse environments, mastering both life in trees and in terrestrial locations (Fleagle, 1998). Because of the variable requirements of these diverse ecological niches, primate movements are consequently complex, exhibiting an impressively large locomotor repertoire. This locomotor complexity relies on the strong hind limbs and mobile forelimbs. The overall mobility of the forelimb depends on the structure and function of the shoulder region (Larson, 1995; Chan, 2007). Consequently, the evolution of shoulder mobility is one of the important evolutionary processes generating the locomotor diversity of primates. The latter is especially relevant among hominoids because within Hominoidea five divergent locomotion modes and associated body plans have evolved (Preuschoft, 2004): arm-swinging in gibbons; forelimb-dominated slow climbing in orangutans; quadrupedalism with climbing in the African apes; mixed bipedal climbing for australopithecines; and bipedal walking in humans. Although the anatomy of the upper limb of apes has been suggested to be adapted for suspensory behaviors (Aiello and Dean, 1990; Larson, 1993; Rose, 1993), some significant differences in limb morphology have also been described that could correspond to differences in locomotion. Even though the locomotor repertoires of non-human apes overlap to a certain extent, the proportions of the different locomotor behaviors and their related kinematics differ between species and hence it is logical to expect that these differences will be reflected in their shoulder morphology. One of the main behavioral dissimilarities is the amount of time that each species spends in arboreal locations. For instance, orangutans and gibbons are predominantly arboreal spending the majority of their time in the canopy (Rodman, 1984), while on the other hand African apes are primarily terrestrial using knuckle-walking when travelling (Hunt, 2004), spending time in the forest canopy to almost exclusively sleep and feed (Hunt, 1992).

The shoulder is a region that in primates functions in rather dissimilar ways in different groups (Oxnard, 1967). It is a pivotal component of the locomotor system as it links the upper limb with the trunk and participates in several ways during different locomotion behaviors (e.g., grasping, climbing, brachiation, among others). Primates exhibit some specific morphological features in their shoulders that distinguish them with respect to other mammals, such as a well-developed clavicle, a dorsally shifted scapula with a prominent acromion and robust spine, and a relatively straight humerus with a globular head (Schultz, 1930, 1961). These traits have usually been related to the high mobility of the arm, and the wide

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excursions of the forelimb. Earlier studies (Oxnard and Ashton, 1962; Ashton and Oxnard, 1963, 1964a,b) showed that forelimb function was related to the degree to which the limb is subject to tensile or compressive forces, being consequently classified based on these results: a) quadrupeds (shoulder subject to mainly compressive forces), b) brachiators (shoulder subject to mostly tensile forces), and c) semi-brachiators (shoulder intermittingly subject to both forces) (Oxnard, 1967, 1968, 1973; Feldesman, 1976; Corruccini and Ciochon, 1978). Following this trend, several authors attempted to relate the observed variability in the primate scapula and associate it with a priori defined locomotor categories by using morphometrics (Miller, 1932; Inman et al., 1944; Davis, 1949; Smith and Savage, 1956; Ashton and Oxnard, 1963, 1964a; Müller, 1967; Oxnard, 1973; Roberts, 1974; Corruccini and Ciochon, 1976; Fleagle, 1977; Kimes et al., 1981; Shea, 1986; Taylor, 1997; Young, 2004, 2006, 2008). These studies have shown that the primate scapular morphology mainly reflects its function; however these analyses do not provide any understanding about the underlying processes relating the scapular form with its function. Although valuable, most of the research about the shoulder girdle have been restricted to morphological comparisons and infrequently aimed to elucidate function from a biomechanical perspective (Preuschoft et al., 2010).

The scapula is anatomically and biomechanically involved in shoulder function and the movement of the arm (Kibler and McMullen, 2003). During daily activities, the shoulder and arm movements required to produce a change in the glenohumeral position are linked. Scapula, shoulder, and arm are either moved into or stabilize in a certain position in order to generate, absorb, and transfer forces that allow movement. Nonetheless, the specific biomechanical function of the shoulder is poorly known when compared to other anatomical locations (Preuschoft et al., 2010). Some classical studies have focused on estimating the force equilibrium for the glenoid cavity of chimpanzees (Preuschoft, 1973), defining basic conditions (Badoux, 1974; Roberts, 1974) and analyzing the functional loadings of the scapula by modeling it as a framework (Müller, 1967). In spite of the practical difficulties involved in observing the movements of the shoulder, some primate taxa have been analyzed (Schmidt and Fischer, 2000; Schmidt, 2005, 2008; Schmidt and Krause, 2011), complementing the observations made earlier by several authors (Stern and Oxnard, 1973; Rose, 1974, 1979; Larson, 1993; Whitehead and Larson, 1994). Preuschoft et al., (2010) applied both armchair biomechanics and 2D finite element models in order to understand the basic functional conditions that occur in the shoulder joint and shoulder girdle of primates. The stress distributions in their hypothetical scapula under the conditions of terrestrial versus suspensory behavior showed that during quadrupedalism the scapula concentrates stress along the cranial margin whereas during suspension generates higher stresses along the axillary border. This would mean that quadrupedal locomotion involves joint forces and muscle activities that would require a long scapula with axillar and cranial margins of a relatively similar length. On the other hand, suspensory behaviors would need a more extended axillary border and a relatively shorter cranial margin in order to provide longer lever arms to the active muscles. Based on their results, they suggested that the forces exerted on the scapula generate, at least partially, its shape (Preuschoft et al., 2010). Indeed, arboreal monkeys seem to have concordant morphological features such as the reinforcement of the axillary border of the scapula and the extension of the infraspinatous fossa (Larson, 1993). This is coherent with all the evidence supporting the idea that bone is functionally adapted to the mechanical demands that are imposed during life (Wolff, 1892; Pearson and Lieberman, 2004).

Nevertheless, other lines of evidence regarding shoulder form and function have found that this relationship is not as clear or straightforward as initially thought (Taylor, 1997; Young, 2003, 2008; Larson and Stern, 2013). It has been found that locomotion differences are not well reflected at an intraspecific level in gorilla scapulae (Taylor, 1997) and that despite locomotion similarities, the scapulae of hylobatids are most similar to those of panids, rather than to those of orangutans (Young, 2008). Furthermore, comparative electromyography data recorded from different apes have shown that there are few differences in patterns of muscle activity among them, consequently suggesting that perhaps hominoids in general use basically similar shoulder mechanisms during locomotion (Larson and Stern, 2013). Unfortunately, there is no clear perspective about the relationship between scapular morphology and its function, in spite of its growing relevance due to recent finding of several hominin scapulae such as *Australopithecus afarensis* (Alemseged et al., 2006; Haile-Selassie et al., 2010; Green and Alemseged, 2012) or *Australopithecus sediba* (Berger et al., 2010; Churchill et al., 2013). In fact, the analyses of these fossils have shown that they tend to resemble the scapula of juvenile gorillas (Green and Alemseged, 2012) or orangutans (Churchill et al., 2013), instead of those of our closest phylogenetic relatives (i.e., panids). Because scapular form has been widely regarded to be primarily a product of shoulder function, it has been a central element in the interpretation of the primate fossil record (Larson, 2007). Understanding how scapular morphology is related to biomechanical performance is important in order to reconstruct the possible locomotor repertoires of extinct species and to appreciate the locomotor diversity observed in extant hominoids.

Nowadays it is possible to produce scientifically accurate virtual reconstructions of primates (Zollikofer and Leon, 2005; Sellers et al., 2010; Ogihara et al., 2011; Weber and Bookstein, 2011). Technological advances in 3D imaging allow the generation of virtual models based on skeletal morphology and comparative soft tissue data obtained from the literature. This is highly useful since the study of primate biomechanics is challenging because traditional experimental techniques are not easily applicable due to practical, conservation, and ethical reasons (Sellers et al., 2010; D'Août and Vereecke, 2011). Computer-based biomechanics comprise 3D quantitate image analysis and simulation techniques applied to musculo-skeletal systems such as finite element analysis (FEA) and multibody dynamics (Sellers and Crompton, 2004; Kupczik, 2008; O'Higgins et al., 2012). FEA is a technique that reconstructs stress, strain, and deformation in material structures and has its origin in mathematical and engineering problems, although it is been increasingly used in biological fields (Rayfield, 2007). This technique is a numerical analysis that acts by dividing a system into a finite number of discrete elements with well-known properties (e.g., triangles, tetrahedrons, or cubes) (Ross, 2005). Strain and stress can be solved by finding analytical solutions if the geometry of the object is simple enough. However, more complex forms may be difficult or even impossible to solve using analytical means, especially if the loading regimens and/or material properties are complex (Beaupré and Carter, 1992). This situation is the most common when dealing with realistic representations of biological structures. FEA offers an alternative approach, approximating the solution by subdividing complex geometries into multiple finite elements of simple geometry. In a structural analysis, typical mechanical parameters of interest are strain, which is the deformation within a structure (Δlength/length; unitless) and stress, the applied force per unit area (Nm^{-2}), which are obtainable as result of FEA (Kupczik, 2008). FEA studies of the scapula have been mostly restricted to orthopedic studies focusing principally on the generation of models of the implanted glenoid (e.g., Friedman et al., 1992; Lacroix et al., 2000; Gupta and van der Helm, 2004; Gupta et al., 2004; Yongpravat et al., 2013; Campoli et al., 2014; Hermida et al., 2014). Even though other FEA studies have been used in comparative primatology and paleoanthropology, they have been predominantly devoted to the analysis of the craniofacial system during mastication (Kupczik et al., 2007; Wroe et al., 2007, 2010; Strait et al., 2009; Curtis et al., 2011; Dumont et al., 2011; O'Higgins et al., 2011; Fitton et al., 2012; Kupczik and Lev-Tov Chattah, 2014). There have been fewer attempts applying FEA to analyze different primate scapulae (Ogihara et al., 2003), so the present study probably represents one of the first analyses of this anatomical structure using an explicit comparative framework.

Morphometrics can be understood as the quantitative analysis of form (i.e., shape and size) and how it covaries with regard to other factors (e.g., biomechanics, development, ecology, genetics, etc.) (O'Higgins, 2000; Adams et al., 2004, 2013). More specifically, geometric morphometrics (GM) refers to the application of morphometrics to coordinate data (i.e., 2D or 3D Cartesian coordinates), normally defined as discrete anatomical loci that are homologous among all the individuals under analysis (Bookstein, 1991; Slice, 2007). GM allows the analysis of the association between morphometric and biomechanical data, which is really useful when studying the relationship between shape and function. There are many available methods to study the connection between morphological and biomechanical variables (e.g., canonical correlation, regression analysis, Mantel test, principal coordinate analysis, and partial least squares, among others). Recent developments in the study of geometric shape and biomechanical modeling have proposed that using both GM and FEA could provide a better understanding of the existing relationship between the shape of skeletal elements and their mechanical performance (Pierce et al., 2008; Piras et al., 2012, 2013; Tseng, 2013). Even though there has been some controversy regarding how to properly combine FEA and GM data (Bookstein, 2013), there is relative agreement that bridging these two techniques could provide interesting insights about the relationship between form and function (O'Higgins et al., 2011; Parr et al., 2012). Because of this reason, different approaches have been proposed to combine FEA and GM data, such as landmark-based analysis in the size-and-shape space of the deformations obtained as result of FEA (Cox et al., 2011; Gröning et al., 2011; O'Higgins et al., 2011; Milne and O'Higgins, 2012; O'Higgins and Milne, 2013), the analysis of finite element models based on warped and target surface meshes (Parr et al., 2012), and the construction of regressions for strain energy density on the largest-scale relative warps (Bookstein, 2013). Besides the issues of how to properly analyze both GM and FEA data, another problem arises when carrying out any biological study containing several species, due to the phylogenetic structure of the data (i.e., non-independence problem). Some approaches have been proposed to take into account phylogeny such as the application of phylogenetic generalized least squares models (PGLS) to fit regressions between matrices of functional/ecological variables and shape variables (Rüber and Adams, 2001; Clabaut et al., 2007; Meloro et al., 2008; Nogueira et al., 2009; Raia et al., 2010; Piras et al., 2013), the use of phylogenetic-independent contrasts estimated for each shape variable before associating them with contrasts derived from functional/ecological variables applying either partial least squares (Klingenberg and Ekau, 1996) or multivariate regressions (Figueirido et al., 2010) and the correlation between morphometric, functional/ecological, and phylogenetic matrices (Harmon et al., 2005; Young et al., 2007; Astúa, 2009; Monteiro and Nogueira, 2010). In the present study, PGLS was preferred because this method is considered more informative and powerful than other methods (e.g., distance matrix correlation) (Peres-Neto and Jackson, 2001).

In this work, FEA was used to analyze the biomechanical performance of different hominoid scapulae by simulating two basic static scenarios: a) quadrupedal standing and b) bimanual suspension. It is expected that scapular mechanical performances will vary depending on the principal locomotion mode of each species. Hence, it is expected that those species that are mostly quadrupedal (i.e., chimpanzees, bonobos, and gorillas) will better withstand the forces generated during quadrupedal standing, while more arboreal species (i.e., orangutans and gibbons) will better bear the forces generated during suspension, as previously proposed (Oxnard and Ashton, 1962; Ashton and Oxnard, 1964a; Roberts, 1974; Preuschoft et al., 2010). On the other hand, GM was used to quantify shape differences, thus comparing different scapular morphologies in relation to their known locomotion regimes. Based on preceding studies (Oxnard and Ashton, 1962; Ashton and Oxnard, 1964a; Young, 2008), scapular shape is expected to reflect mostly functional demands instead of phylogenetic relationships. Finally both FEA and GM were used to study the relationship between form and function by applying both multiple multivariate regressions and PGLS regressions. Our results are expected to contribute to a better insight of the association between hominoid scapular morphology and its biomechanical performance.

MATERIALS AND METHODS

Sample

CT-scan stacks of 11 different hominoid individuals obtained from online databases and two zoos were analyzed (Table 1; Fig. 1) (for further details about the sample see Supporting Information 1). The included species were *Hylobates lar, Pongo abelii*, *Pongo pygmaeus, Gorilla gorilla, Pan paniscus*, *Pan troglodytes*, and *Homo sapiens*. All the specimens were adult with no evident or reported pathologies associated with their shoulder girdles. Only left scapulae were modeled, although due to some CT artifacts, some right scapulae were reflected to be used in the subsequent analyses.

Finite element modeling

Segmentation. The first step to build a model from a CT stack is to carry out image segmentation. This procedure basically consists in extracting the material of

TABLE 1. Sample

Species	Common name	Accession number	Origin	Sex	Number of elements
Pan paniscus	Bonobo	Desmond	The Royal Zoological Society of Antwerp	Male	953156
Gorilla gorilla	Gorilla	Willie (GAIN 23)	Digital Morphology Museum (KUPRI)	Male	931087
Pan troglodytes	Chimpanzee	9266	Digital Morphology Museum (KUPRI)	Male	936693
Pan troglodytes	Chimpanzee	9783	Digital Morphology Museum (KUPRI)	Female	952156
Pan troglodytes	Chimpanzee	10048	Digital Morphology Museum (KUPRI)	Female	950295
Pongo pygmaeus	Bornean Orangutan	Satsuki (GAIN 37)	Digital Morphology Museum (KUPRI)	Female	996480
Pongo abelii	Sumatran Orangutan	9653	Digital Morphology Museum (KUPRI)	Male	935358
Homo sapiens	Human	Visible human female	The Visible Human Project	Female	962225
Homo sapiens	Human	Visible human male	The Visible Human Project	Male	985562
Hylobates lar	White-handed Gibbon	3308	National Museum of Scotland	Male	940973
Hylobates lar	White-handed Gibbon	3508	National Museum of Scotland	Female	939611

interest (in this case bone) out of the surrounding background and tissues where it is embedded. The CT-scans of the different hominoid species were segmented; DICOM files were imported into Seg3D v. 2.1 (CIBC, USA) where each specimen was segmented by applying a combination of case-specific thresholding values and manual painting techniques. Scapulae can be complicated to segment because their blade is extremely thin at certain areas. As a result all the models were dilated one extra voxel, to avoid possible holes in the mesh that could affect the FEA results. After performing this procedure and manually checking the results, the extra voxel layer was removed by using an erode function in the same software. The scapulae were modeled as solid parts composed only by cortical bone. Surfaces were then generated and exported as .STL files into Geomagic Studio v. 12 (Geomagic, USA). Using this software, possible errors in the polygon mesh were detected and corrected in order to remove protruding vertices and localized holes. The models had dissimilar number of elements derived from the differences in the original scan resolution; therefore they were decimated to a number of elements ranging from 20,000 to 25,000 mesh triangles. All the models were globally remeshed to simplify their element geometry, keeping the number of mesh triangles in a similar number range (i.e., 20,000–25,000). The remeshing process was applied to generate a more homogenous mesh in terms of the shape of the triangles, their distribution on the surface, and their connectivity. In addition, one individual was selected as a reference to perform a best-fit alignment using the same software in order to align all the models with respect to a common reference plane. This procedure was carried out prior to FEA to align all the models, so that loads could be applied in the same axis and to allow easier interpretation of stress results. Basically, the procedure consisted in fitting two scapula models at each time by measuring from point to point and adjusting the location of the target model to the stationary reference specimen until the average deviation was as low as possible using an iterative process (sample size: 10,000). The sums of squares of the distances between the sample pairs were minimized over all the rigid motions that could realign the two models to achieve the best-fit alignment of them. This procedure was repeated for each one of the analyzed specimens. The models were then exported as .OBJ files into Autodesk 3ds Max 2012 (AutoDesk, USA), where they were converted into .SAT files. The models were then imported into Abaqus v. 6.13 (Simulia, USA) as closed manifold solid parts in order to carry out an implicit static FEA. Finite element validation analyses have shown that both four-node and eight-node tetrahedral, and mixed four-node tetrahedral and eight-node hexahedral meshes perform well when compared with experimental data (Panagiotopoulou et al., 2011). Likewise, it has been shown that meshes composed by more than 200,000 elements show negligible stress differences between models with four- or ten-node tetrahedra elements (Brassey et al., 2013). Because ten-node tetrahedra are computationally more expensive than those composed by four nodes, the surfaces were meshed using four-node tetrahedral elements (C3D4) by applying a built-in Delaunay meshing algorithm in Abaqus v. 6.13. FE meshes were verified in the same software to find poor-meshed areas or low quality elements (i.e. aspect ratio >10). When found, those areas were re-meshed to improve mesh quality.

Material properties and boundary conditions. Many researchers are currently trying to produce more accurate finite element models by incorporating more detailed information such as muscle activation data, anisotropic material properties, several different tissues with dissimilar material attributes, etc. (Ross et al., 2005; Strait et al., 2005; Kupczik et al., 2007; Gröning et al., 2011; Rayfield, 2011). These kinds of analyses have shown that when this type of information is included, the correlation between simulations and experimental data is usually increased. Nevertheless, in this work FEA was used in a comparative fashion rather than being used to validate the models. Because of the fact that hominoid scapulae are relatively uncommon (belonging most of the time to museum specimens), destructive experimental mechanical approaches are

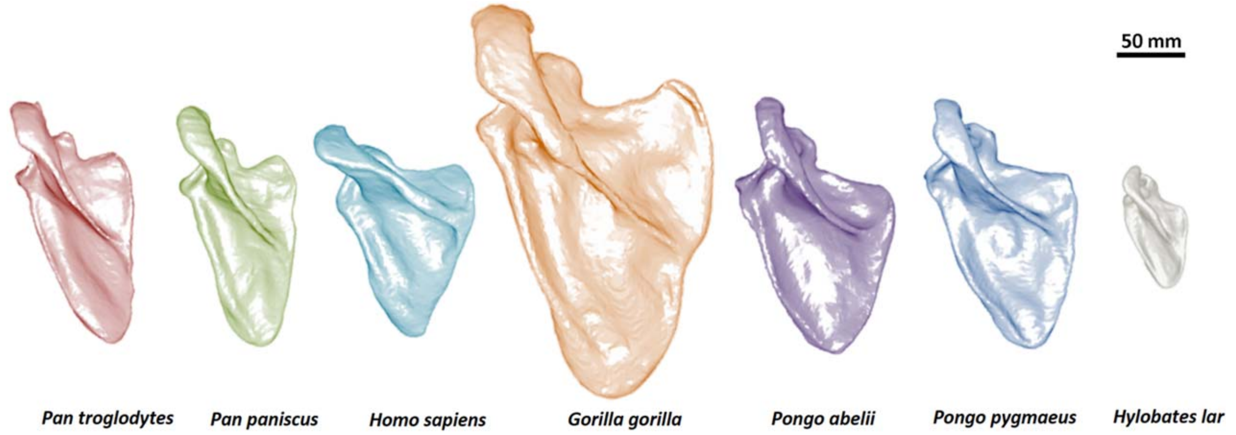

Fig. 1. Three-dimensional volumetric models of the hominoid scapulae considered in this study. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

typically difficult or impossible to perform. The present study therefore applied FEA as a structural comparative technique rather than trying to specifically recreate how the hominoid is loaded during life; the idea was to compare a general measure of mechanical performance taking into account phylogenetic relationships. Furthermore, living specimens would probably withstand the tensile strain and stresses experienced during locomotion mostly on their shoulder soft tissues such as muscles, ligaments, and tendons rather than directly on their scapulae. Even though shoulder muscle origin and insertions for hominoids are known (Diogo et al., 2010,2012,2013a,2013b; Diogo and Wood, 2012) and physiological cross-sectional areas of some the muscles are available for some of the analyzed species (Veeger et al., 1991; Keating et al., 1993; Thorpe et al., 1999; Cheng and Scott, 2000; Carlson, 2006; Oishi et al., 2008, 2009; Michilsens et al., 2009; Peterson and Rayan, 2011; Myatt et al., 2012), the specific activation patterns are unknown for the majority of the species when performing the analyzed postures. These reasons ratified the decision of carrying out simpler comparative structural analyses instead of simulating in detail loading scenarios based on unknown or uncertain information. This means that the current work can be better understood as an analysis of how the mechanical behavior of the hominoid scapula is related to its shape, rather than being a highly-realistic simulation of how the scapula is loaded in vivo.

After the construction of the finite element mesh, it was necessary to specify the mechanical properties of the elements composing the specimens. Even though several material properties for primate cortical and trabecular bone have been published especially for humans (e.g., Currey and Butler, 1975; Williams and Lewis, 1982; Currey, 1988; Dechow et al., 1993; Ding et al., 1998; Zysset et al., 1999; Margulies and Thibault, 2000; Phelps et al., 2000; Dechow and Hylander, 2000; Peterson and Dechow, 2003; Havill et al., 2003; Bayraktar et al., 2004; Kaneko et al., 2004; Wang et al., 2006a,b; van Eijden et al., 2006; Hofmann et al., 2006; Kupczik et al., 2007; Daegling et al., 2009), there is almost a total absence of material property values for the analyzed hominoid scapulae. We used rough average values for mammalian-longitudinal cortical bone samples (Currey, 2002) (Young's modulus: 18 GPa; Poisson's ratio 0.3). The scapulae were modeled as solid models composed only of cortical bone in order to simplify the analyses, as well as to limit the number of assumptions. In fact, recent evidence has shown that FEA applied to specimens with unknown internal architecture can produce reliable results, even when the internal bone architecture cannot be modeled in detail (Fitton et al., 2015). In addition, scapulae do not exhibit high internal complexity in comparison with other bones, because most of the scapular blade consists of only a thin layer of compact tissue (i.e., cortical bone). Although bone generally behaves anisotropically, it was modeled as a linear elastic and isotropic material due to the same reasons outlined above. Besides, it has been shown that isotropic modeling seems to have little effect compared to anisotropic modeling on the pattern of stress (Chen and Povirk, 1996; Strait et al., 2005). Apart from assigning material properties, it was necessary to define boundary conditions (Bhatti, 2005). Two essential boundary conditions were specified; one recreating the action the rhomboideus, and another simulating the constraint imposed by the serratus anterior, as shown in Figure 2a. It was decided to constrain these areas because in both quadrupedal and suspensory situations the forces applied to the shoulder region seem to be predominantly supported by the muscles attached to the vertebral border of the scapula (Badoux, 1974). In these areas the displacements were only constrained in the z-direction in both cases because the forces were applied only in that direction. These boundary conditions were defined to prevent rigid body motions of the geometry and counteract residual moments (from errors when applying the loadings), but without over-constraining the models.

Loading scenarios. The scapula is one of the most complex bones of the primate skeleton due to its particular shape and because it is subjected to a great variety of forces from attached muscles during its movement (Roberts, 1974; Aiello and Dean, 1990). This bone is subject to a number of muscle, ligament, and joint reaction forces during elevation of the arm, that are difficult to quantify (Bagg and Forrest, 1986; Johnson et al., 1996; Kibler and McMullen, 2003; Fayad et al., 2006; Amadi et al., 2008; Bello-Hellegouarch et al., 2013). Quantitative and qualitative estimates of all the muscles, ligaments, and joint reaction forces acting on the human scapula during humeral abduction have shown that the scapula is relatively loaded all over its structure during abduction (van der Helm,

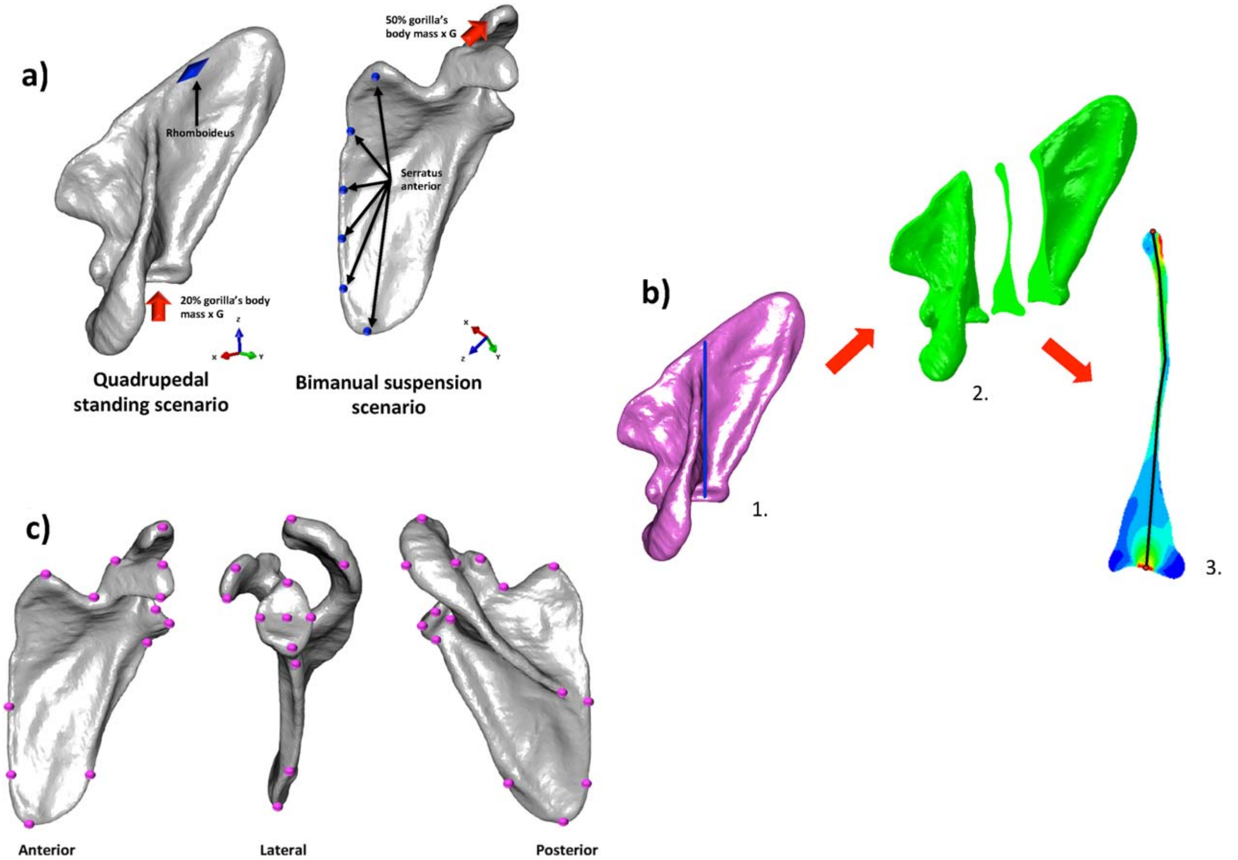

Fig. 2. *Pan paniscus* scapula used to depict **a**) FEA loading scenarios: the red arrows represent the force vectors and their direction, while the blue shapes represent the applied constraints. The constraints representing the action of serratus anterior and rhomboideus muscles were applied in both the quadrupedal standing and bimanual suspension scenarios by limiting displacement in the *z*-axis; **b**) Extraction method of the stress values: 1) At the center of the glenoid cavity a slice on the *x*-axis was defined (blue line), 2) this slice was separated and 3) two coordinates at each extreme of the slice (red dots) were used to define a path (black line) divided in 101 equidistant points used to extract von Mises stress values; **c**) 3D landmarks used to perform GM analyses. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

1994; Gupta and van der Helm, 2004). It is therefore extremely difficult to define realistic loading scenarios and necessary to simplify the load cases in order to avoid excessive assumptions.

One important consideration to take into account when analyzing different individuals using FEA is how to make the obtained results comparable. Strain energy is proportional to the square of the load and to volume (Dumont et al., 2009), hence it is important to account for size differences when performing strain energy comparisons. Several solutions have been proposed to compare total strain between different specimens. Suggestions include scaling the loads to yield similar force:surface area ratio or scaling them to a relevant biological measurement (e.g., bite force, moment arm, animal weight) (Fitton et al., 2012; Parr et al., 2012; Brassey et al., 2013). Another possibility is to scale the models to achieve the same surface area or same volume, or to simply scale the obtained results from the analysis with respect to a sensible measure (Dumont et al., 2009). In the present work, it was decided to normalize scapular size by volume while applying the same forces to all the individuals during the FEA. This decision was based on the fact that this approach seems more suitable to evaluate how scapular shape affects mechanical strength. All the scapulae were scaled to have the same volume as the gorilla specimen (i.e., 387810.84 mm^3) in Geomagic Studio v. 12 (Geomagic, USA), and depending on the specific loading scenarios, different percentages of the reported body weight of the gorilla specimen (i.e., 176 kg) were applied to simulate the mechanical loadings. The biomechanical performance of different hominoid scapulae was tested in two basic static scenarios (Fig. 2a).

Quadrupedal standing: African apes predominantly use knuckle-walking when travelling. According to Hunt (2004), terrestrial quadrupedalism represents 96% of the locomotor behavior in mountain gorillas, 64.4% in lowland gorillas, and 35.3% in bonobos, but only 9.9% in chimpanzees. African ape scapular morphology is therefore expected to show clearer adaptations to terrestrial quadrupedalism. It is important to take in to account that chimpanzees and other primates support most of their body mass on their hind limbs during quadrupedalism rather than on their forelimbs (Reynolds, 1985; Kimura, 1992; Demes et al., 1994; Li et al., 2004; Raichlen et al., 2009). Nonetheless, due to the greater use of terrestrial locomotion modes in the African apes than in orangutans or gibbons, it is reasonable to expect that their forelimbs would be less specialized for arboreal behaviors. Even though African apes do use suspensory behaviors as a static postural activity, it is likely their scapulae are not as specialized for more recurrent suspensory behaviors such as those observed in gibbons and orangutans.

Although adult humans do not use their forelimbs for quadrupedal locomotion, the same loading scenario was applied for comparative purposes. Hominoid forelimbs support about 40% of the body weight during terrestrial quadrupedalism (Reynolds, 1985; Kimura, 1992; Demes et al., 1994; Li et al., 2004; Raichlen et al., 2009). Hence, the total applied load was calculated as 20% of the gorilla's body mass Mb; kg) multiplied by gravitational acceleration (G: 9.81 m s^{-2}), because only one scapula was analyzed per individual. This yielded a total force vector of 345.31 N., which was directed towards the center of the glenoid cavity in the *z*-axis, and applied in 24 nodes (total force/24 nodes). In addition, two models (one gibbon and the gorilla) were selected to carry out additional simulations to the test the sensitivity of the results to small differences in the application angle of the load vector, so it was changed in 5°. The results were extracted according to the procedure described in Figure 2b and a correlation was estimated to assess the level of concordance between the original stress values and those obtained after changing the load vector (Gibbon: R^2: 0.981, *P* value: <0.001; Gorilla: R^2: 0.969, *P* value: <0.001) . Therefore, the results seem to be robust to at least small changes in load direction.

Bimanual suspension: Arm-hanging is probably the only common ape posture requiring complete abduction of the arm (Hunt, 1991a,b,1992,2004). It has been suggested that the cranially oriented glenoid fossa observed among apes may be adaptive to distribute strains more evenly over the glenohumeral joint capsule during arm-hanging (Hunt, 1991b,). The long and narrow scapular shape exhibited by apes has been hypothesized to increase the mechanical advantage of the trapezius and serratus anterior during the scapular rotation necessary for arm-raising (Ashton and Oxnard, 1963, 1964b; Oxnard, 1967). However some hominoid species probably use this locomotor behavior more often than others. For instance, the highly arboreal gibbons and orangutans are expected to better cope with strains derived from this posture than the more quadrupedal species.

Even though earlier studies (Roberts, 1974; Tuttle and Basmajian, 1978) suggested that no scapulohumeral muscle was activated during bimanual or unimanual hanging assuming that joint integrity was kept solely by osseoligamentous structures, new evidence have proved the contrary. Opposed to the common idea that no muscle activation is required while the body is suspended beneath the hand (likely causing transarticular tensile stress at the glenoid cavity), hominoid electromyography data during bimanual hanging has shown that there is a continuous activity in the infraspinatous, posterior deltoid, and teres minor muscles (Larson and Stern, 1986; Larson and Stern, 2013). It has been pointed out that when climbing or hanging, primates activate the levator scapulae and trapezius muscles to prevent the caudal movement of the scapula (Larson and Stern, 1986). The resulting dorsal rotation of the caudal angle of the scapula is counteracted by the action of the caudal portion of the serratus anterior (Larson and Stern, 2013). This implies that the scapula seems to achieve its equilibrium during suspension by the coordinated action of levator scapulae and cranial trapezius, as well as the caudal serratus (Larson and Stern, 1986). In addition, to avoid the pulling of the scapula in a ventral direction, the activity of the caudal portion of the trapezius is required (Larson et al., 1991). In fact it has been observed that this muscular portion is prominently developed in apes (Aiello and Dean, 1990). It has been also mentioned that some of the forces applied to the shoulder region during suspension are supported by the muscles attached to the vertebral border of the scapula (i.e., serratus anterior and rhomboideus) (Badoux, 1974). The models were loaded in a simpler scenario by applying total load estimated as 50% of the gorilla's body mass Mb; kg) multiplied by gravitational acceleration (G: 9.81 m s^{-2}), because the total animal weight was supported by the two shoulders, thus yielding a total force vector of 863.28 N. This tensile force vector was directed away from the acromion in the *z* axis and it was also applied on 24 nodes (total force/24 nodes).

Solution. After defining the material properties and establishing the boundary conditions, the models were submitted into the Abaqus implicit solver. Each specimen was subjected to two different simulations: a) quadrupedal standing and b) bimanual suspension. Stress values were obtained and exported as .CSV files.

Statistical analyses of FEA results. von Mises stress values were obtained from 101 locations extracted along a path as described in Figure 2b. Starting from the center of the glenoid a slice on the *x*-axis was selected. Two points were defined at each opposite extremes of the slice and between these two coordinates a path was established where 101 equidistant points were positioned to extract stress values. These values were imported into R v.3.1.3 (http://www.R-project.org/) to carry out statistical analyses. The average values per species were calculated for each one of the locations. To visualize these results, a UPGMA clustering was estimated by calculating the Euclidean distances between species using the hclust() function of the package "stats." In addition a Principal Components Analysis (PCA) was performed using the princomp() function of the same package in order to reduce the number variables of this high dimensional dataset, and to subsequently perform the multivariate multiple regressions and the PGLS regressions. Because of the fact that the obtained stress could have values that differ in orders of magnitude between anatomical loci, the PCA was carried out based on the correlation matrix to standardize these possible scale differences. The number of PCs used in the successive analyses was selected to account for ca. 95% of the total variance of the sample.

Geometric morphometrics

The 3D surface models were imported into the R package "geomorph" where 20 homologous landmarks were collected on each one of the analyzed specimens using the digit.fixed() function (Adams and Otárola-Castillo, 2013) (Fig. 2c). All the GM analyses were carried out in the same package. A generalized procrustes analysis was applied to extract the shape variables from the raw landmark data, by removing all the differences due to translation, rotation and scale (Bookstein, 1991). The average shape and biomechanical performance was estimated for each species and used in the subsequent analyses. A PCA of the procrustes coordinates was performed in order to find the orthogonal axes of maximal variation, thus allowing the visualization of scapular shape variation. A consensus phylogeny (described below) was projected onto the space identified by the first two PCs obtained from the covariance matrix of the average shapes of the analyzed taxa. Using this consensus phylogeny, both morphological (i.e., shape variables) and biomechanical (i.e., stress values)

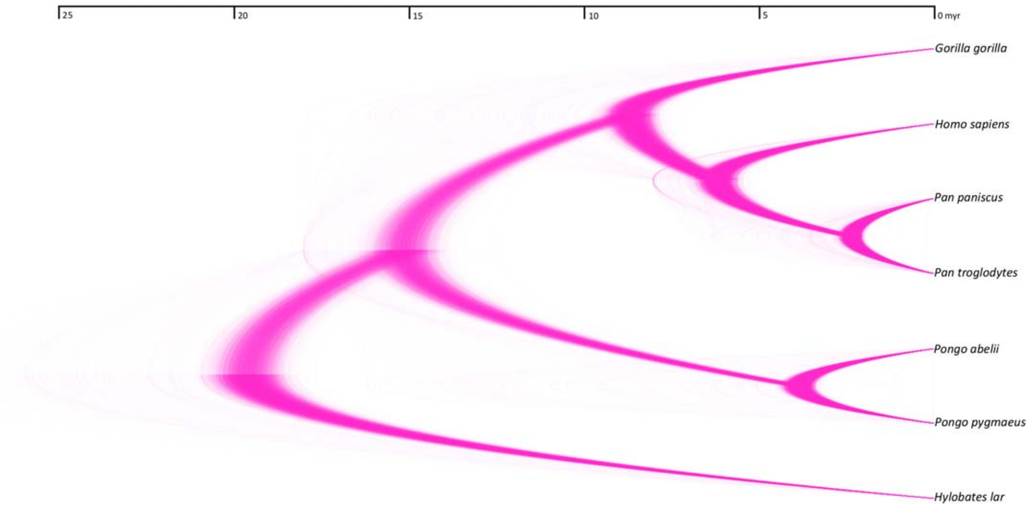

Fig. 3. 10,000 molecular phylogenetic trees plotted to overlap on top of each other in order to represent the evolutionary relationships of the analyzed taxa. The high density of the main branches is indicative of a high consistency between trees. The consensus tree was estimated and used in the subsequent comparative analyses. The plot was generated using DensiTree 2.01 (Bouckaert, 2010) and the phylogenies were obtained from the 10KTrees website (http://10ktrees.fas.harvard.edu/Primates/index.html). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

phylogenetic signal were estimated using a generalization of the Kappa statistic suitable for highly multivariate data using the physignal() function (Blomberg et al., 2003; Adams, 2014). This method, denominated as Kmult, is based on the equivalency between statistical methods based on covariance matrices and those based on distance matrices, thus allowing a convenient way to assess phylogenetic signal in high-dimensional multivariate traits, such as those analyzed here (Adams, 2014). The K-statistic varies between 0 (no phylogenetic signal in the data, for instance with a star phylogeny) to 1 or more (data fit a Brownian motion model of evolution) (Blomberg et al., 2003). To analyze the relationship between shape and function a multiple multivariate regression of shape variables and stress PC scores was performed using the procD.lm() function. Subsequently, in order to examine the relationship between morphology and biomechanical performance taking into account the phylogenetic structure of the data a PGLS regression of shape variables and stress PC scores was performed using the procD.pgls() function. The idea in both cases was to evaluate the amount of shape explained by functional demands (Piras et al., 2013). The PGLS regressions were carried out using the procD.pgls() function. It is important to consider that the phylogenetic covariance matrix is just a 7 × 7 matrix, which is a limitation. In previous methodological papers (e.g., Blomberg and Garland, 2002; Blomberg et al., 2003), it has been suggested that about 15–20 OTUs are the minimum to have an acceptable statistical power, hence the obtained results have to be cautiously considered. All the aforementioned analyses were carried out in R v. 3.0.3. (http://www.R-project.org/).

Phylogeny

Using the 10kTrees Website (http://10ktrees.fas.harvard.edu/Primates/index.html), 10,000 phylogenies of the analyzed hominoid species were downloaded using the third version of this dataset (Arnold et al., 2010) (Fig. 3). These phylogenies were sampled from a Bayesian phylogenetic analysis of molecular data for eleven mitochondrial and six autosomal genes that were available in GenBank (Arnold et al., 2010). The advantage of using the 10kTrees dataset that it allows the generation of a set of phylogenetic trees suitable for comparative research that actually reflects uncertainty levels in the understanding of phylogenetic relationships, as well as providing a robust way to test phylogenetic relationships. The consensus tree of these 10,000 phylogenies was estimated and used in the subsequent comparative analyses.

RESULTS

FEA

All the analyzed individuals showed a stress widely distributed on the scapular blade, although it was logically higher in the locations where the constraints were placed (Fig. 4) (the stress values used in the analyses are available in the Supporting Information 2). The suspension scenario logically showed greater stress values (mostly on the acromion) than the quadrupedal standing simulation, due to the fact that higher loads were applied. *Hylobates lar* experienced the lowest stress for both loading scenarios when compared with rest of the hominoids, while the gorilla specimen showed the highest stress values. Interestingly, the pongids showed relatively high stress values for the standing scenario, while exhibiting relatively similar values to the gibbons during the suspension scenario. Biomechanical performance measured as von Mises stress also showed significant phylogenetic signal (quadrupedal standing, Kmult: 0.73; *P* value: 0.022; 10,000 perm. and bimanual suspension, Kmult: 0.67; *P* value: 0.042; 10,000 perm.). The UPGMA clustering of the standing scenario partially followed the hominoid phylogeny, although the gibbon and the gorilla were in reverse positions. On the other hand, UPGMA clustering of the suspension scenario showed that the suspensory species grouped together with lower stress values as compared with the rest of specimens.

GM

Phylogenetic signal was found for shape (Kmult: 0.74; *P* value: 0.007; 10,000 perm.) but not for centroid size (Kmult: 1.09; *P* value: 0.07; 10,000 perm.). Regarding shape

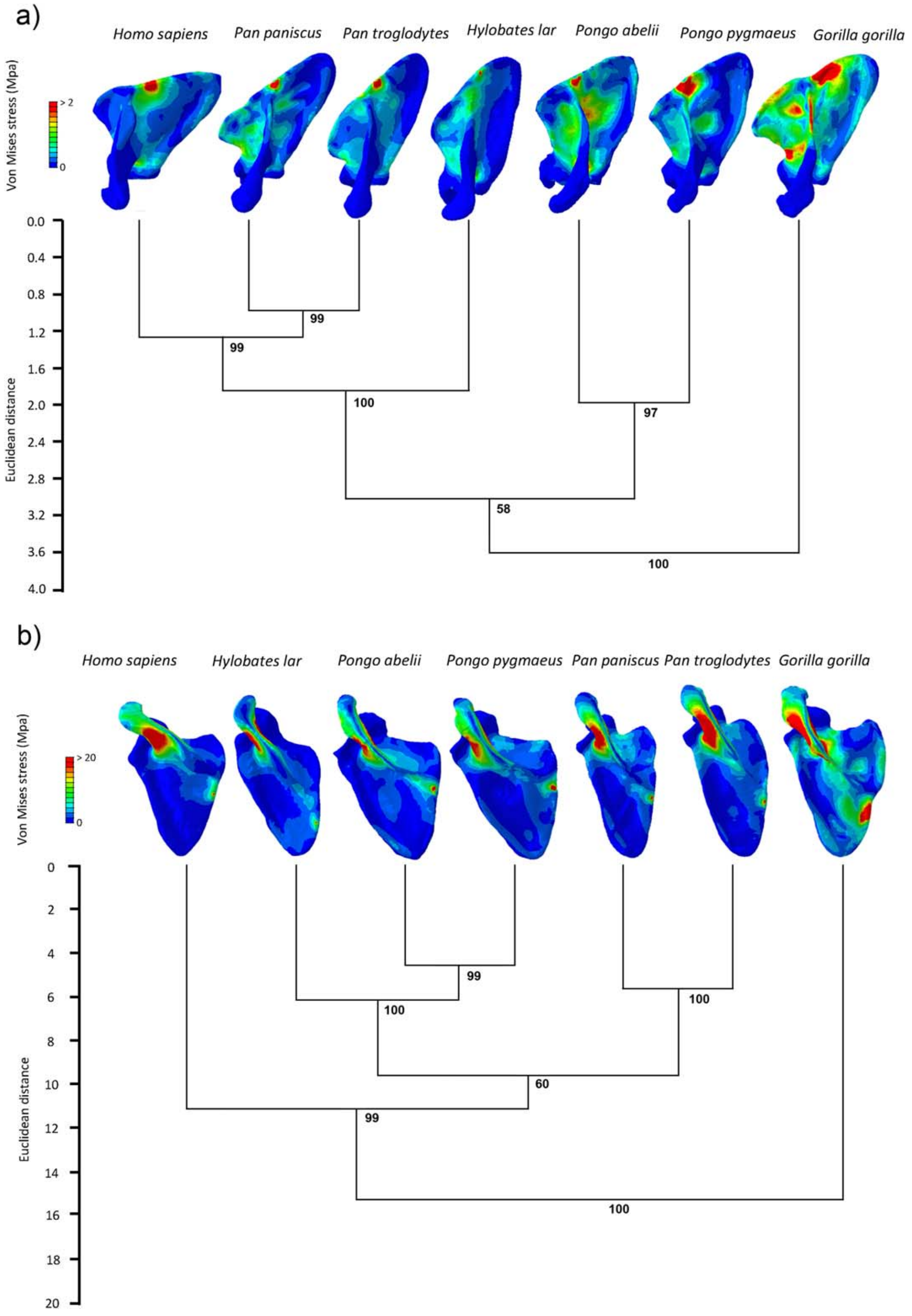

Fig. 4. UPGMA dendrogram of the von Mises stress values extracted from the different scapulae: **a**) quadrupedal standing and **b**) bimanual suspension. Bootstrap values at nodes were calculated after 10,000 permutations. Above each dendrogram the finite element models were drawn to depict the distributions of von Mises stress observed in the different hominoid scapulae. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

(Fig. 5), the lack of overlapping branches of the phylogeny projected onto the shape space seems to imply that there is little evidence to support convergent evolution in the hominoid scapular shape, although further tests are required. The variation along PC1 could be described as more slender shapes at the positive side (e.g., *Hylobates lar*; *Pan troglodytes*) while the scapular morphologies occupying the negative side were relatively wider (e.g., *Homo sapiens*). Interestingly, *Homo* and *Pongo* morphology seem to be the most divergent compared to the other nonhuman

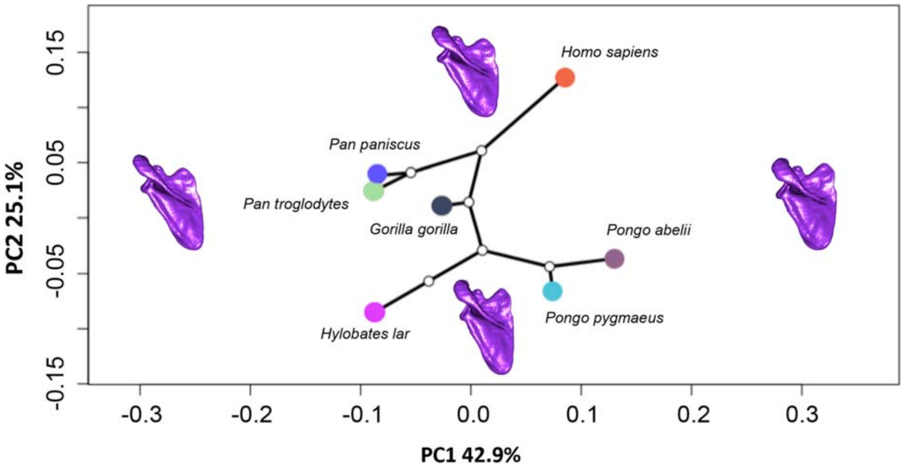

Fig. 5. Phylomorphospace of the hominoid scapular variation. The first two principal components (PCs) were used to display the majority of the morphological variation, while the projected phylogeny shows the evolutionary relationship between the analyzed taxa. The scapulae models were used to depict morphological variation along the PC axes. The model closest to the mean shape was warped to match the multivariate mean using the thin plate spline method (Bookstein, 1991). Then the obtained average model was warped to represent the variation along the two plotted PC axes. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

hominoids. The multiple multivariate regressions of shape variables on the stress PC scores showed that there is significant relationship between scapular morphology and biomechanical performance (quadrupedal standing: adjusted-R^2: 0.79; F: 5.5918; P value: 0.022; bimanual suspension: adjusted-R^2: 0.63; F: 3.5333; P value: 0.006; 10,000 permutation rounds). However, only the PGLS regression of shape variables on the PC scores of the standing scenarios stress values was significant (quadrupedal standing: adjusted-R^2: 0.26; F: 1.4212; P value: 0.044; bimanual suspension: adjusted-R^2: 0.21; F: 1.4066; P value: 0.074; 10,000 permutation rounds). The low adjusted R^2 values are partially explained due to the reduced sample size, hence these results must be cautiously considered.

DISCUSSION

Previous studies have shown that primate scapular morphology is primarily related to positional behavior and/or movement needs (Oxnard, 1998). In fact, scapular morphological variation has been interpreted as being a reflection of the functional demands related to particular locomotion requirements (Inman et al., 1944; Oxnard, 1969; Radinsky, 1987; Larson, 1993; Hildebrand and Goslow, 1998). However, it is still not completely clear what the relationship is between scapular form and function. This question is relevant in order to address whether scapular shape reflects mostly functional or phylogenetic signals, because it has been frequently assumed that the postcranium is the product of stronger functional signals rather than containing phylogenetic information (Pilbeam, 1996, 2004; Ward, 1997; Lockwood, 1999; Collard et al., 2001). This assumption can lead to profoundly biased evolutionary reconstructions, in spite of the cumulative evidence that demonstrates the significant phylogenetic structure in mammalian postcrania (Sánchez-Villagra and Williams, 1998; Young, 2003, 2005). In spite of the widespread idea that the scapular morphology mainly reflects functional demands, our results showed that shape exhibited significant phylogenetic signal. This means that closely-related species tend to show similar trait values due to their common ancestry. This is consistent with more recent research that proposed within the functional structure of the scapula there is phylogenetic signal as well (Young, 2003, 2008). Although Young (2008) states that this phylogenetic signal is particularly noticeable at infant stages, we were able to clearly identify it in adult scapulae. The FEA results also showed significant phylogenetic signal, thus closest related species tended to show similar stress values in both loading scenarios, as broadly observed in the UPGMA clustering. However, as previously mentioned these results have to be carefully considered due to the reduced number of analyzed OTU's. It is necessary to increase the phylogenetic extent of this analysis including more anthropoid species so that the analysis can be more robust.

The FEA results showed that most species seem to behave relatively similarly under the two loading scenarios, with gibbons exhibiting the lowest stress levels, probably because their scapulae have to cope with the elevated stresses resulting from their highly demanding locomotion mode. Because of the fact that material properties were the same for all the models and that the same load was applied to all the specimens after scaling them to the same volume, it is possible to suggest that the particularly different scapular morphology of the gibbons could be the main factor reducing the experienced stress. Even though the locomotor morphology of gibbons is qualitatively similar to the anatomy of the other hominoids (Swindler and Wood, 1973), the highly suspensory locomotion mode of the gibbons has contributed to certain specialized anatomical features such as an axially elongated scapula (Takahashi, 1990). This could imply that their particular scapular morphology is adjusted to support their highly demanding locomotion habits. Interestingly, orangutans showed relatively higher stress values in the standing scenario but relatively lower values in the suspension case (similar to the gibbon values). Perhaps the slow climbing locomotion mode observed in these animals could explain this observation, because these species are noticeable slower and less acrobatic than the other hominoids. However, it is necessary to include a broader sample of primate species in order to test this issue in a more comprehensive and robust manner.

The FEA results also showed that for the two analyzed loading scenarios, the stress was relatively distributed all over the scapular blade, although logically the higher localized areas were the locations where the forces were applied and where the constraints were positioned. This result is consistent with quantitative and qualitative studies that have shown that the scapula is relatively loaded all over its structure (van der Helm, 1994; Gupta and van der Helm, 2004). However in the suspension scenario higher loads were observed in the acromion. Epidemiological reports in human populations have shown that scapular fractures are extremely uncommon, showing the lowest incidence among all fractures, normally requiring exceptionally large amounts of energy to be affected (e.g., motor vehicle accidents) (van Staa et al., 2001). Of the different fractures that affect the bony components of the shoulder girdle, clavicle fractures are significant and notoriously more common (Armstrong and Van der Spuy, 1984; Nordqvist and Petersson, 1995). The scapula is wrapped by soft tissue and the clavicle tends to fracture more frequently, suggesting that when the scapula is loaded an important portion of the load is transmitted to the clavicle that seems to behave as a strut. The present FEA models are consistent with this possibility showing higher stress value at the scapular spine when they are "pulled" upwards such as in the suspension scenario.

The phylomorphospace (Fig. 5) showed that scapular shape seems to be consistent with the phylogenetic history of the group, thus morphological variation seems to relatively follow the evolutionary history. The absence of overlapping branches in the phylomorphospace suggests that scapular shape variation does not exhibit evident convergent evolution, however further analyses are required. Humans and orangutans showed the most divergent morphologies when compared to the rest of the hominoids (they were mostly distinguished by PC1, which accounted for 42.9% of the scapular shape variation). The morphological variation along this axis could be described as more slender shapes at the negative side (e.g., *Hylobates lar*; *Pan troglodytes*), while the scapular morphologies occupying the positive side were relatively wider (e.g., *Homo sapiens*, *Pongo abelii*). On the other hand, PC2 seems to separate between more arboreal species (i.e., orangutans and gibbons) and the rest of the hominoids. The morphological variation along this particular axis is associated with a scapular spine that points upwards in the negative portion of the axis, while the upper part exhibits morphologies that tend towards more horizontal spines. Additionally, the shapes occupying the negative side of the axis present different morphologies of the superior angles in comparison with those located on the positive side. This area provides the attachment site for some fibers of the levator scapulae muscle, thus suggesting different loading regimes of this muscle when elevating the scapula between arboreal and non-arboreal hominoid species.

There was a significant relationship between scapular shape and biomechanical performance both for the multiple multivariate regressions and when phylogenetic nonindependence was taken into account by performing the PGLS regression (excepting the suspension scenario, which was almost significant for this latter test). This means that there is relationship between scapular shape and its function, with at least part of the scapular shape variation due to non-phylogenetic factors, probably related to functional demands. This is logical, because the mechanical behavior of a structure depends on the combination of the geometry (i.e., shape) and the material properties that constitute the structure itself. Nonetheless, it is important to interpret all these results with caution, due to the small sample size used here. Further studies should increase the analyzed specimens to generate more robust statistical analyses. Interestingly, the most slender specimens (i.e., hylobatids) showed lower stress levels compared to the rest of the hominoids. In fact, hylobatids are clearly distinguished from other hominoids by a very angled spine and small infraspinous and supraspinous fossae. These specific differences might reflect gibbon adaptations to the highly specialized hylobatid locomotion (i.e., brachiation). Nonetheless, it is intriguing that gibbons and chimpanzees are distinguished along PC2, occupying almost the same position in PC1. Along this axis there is an overall similarity between panids and hylobatids. Both groups posses a narrow scapula from the vertebral border to the glenoid, with short and more acutely angled spine relative to the axillary border. The similarities suggest that these morphological traits could be an ancestral condition of apes, or could have arisen as convergent traits due to common function. Nevertheless, there are few specific locomotor similarities between panids and hylobatids, once the arboreal and suspensory adaptations shared also with *Pongo* and *Gorilla* are excluded. The analyses also revealed that *Homo* exhibit a derived morphology expressed in a relatively broader blade, probably associated with the fact that humans normally do not extensively use their arms during locomotion in comparison with the rest of the hominoids. Perhaps the biggest loads on human shoulders might relate to carrying, then being consequently tensile and complex. Human scapulae occupy the opposite morphological position of gibbons in the morphospace both in PC1 and PC2, suggesting a scapular shape possibly devoted to less demanding biomechanical regimens.

Interestingly, the scapula of *Pongo* seems to be distinct compared to the rest of hominoids (Young, 2003, 2008). The present study has also shown that this genera stands out when compared to the other hominoids due to its outlier position in the different analyses that were carried out. They have a scapular shape unique among the hominoids, which can be described as a combination of suspensory and quadrupedal characteristics. This trait combination is interesting; because orangutans are highly arboreal and suspensory, but these characters seem to suggest a closer morphological affinity to arboreal quadrupeds (Young, 2008). This distinctive morphology seems to combine both traits that have been traditionally associated with quadrupeds (e.g., glenoid greatest width caudally located and a scapular spine that extends to the vertebral border) and others that are typical of non-quadrupedal species (e.g., a cranially oriented glenoid cavity and long scapular shape blade that is also cranially oriented). The pongid scapular spine is comparatively robust, thus suggesting a larger trapezius attachment compared with the other hominoids. Nevertheless, its glenoid cavity seems to be more similar to the quadrupedal condition, although lacking the distinct lip that supposedly limits limb mobility during forelimb extension (Larson, 1993). A possible explanation for this singular morphology is that forelimb-dominated slow climbing in orangutans could be related to these anatomical features, because they use more cautious pronograde suspensory behaviors compared to the rest of the African apes (Thorpe and Crompton, 2005, 2006). The particular shoulder morphology of orangutans could be related to suspensory postures and locomotion that imply placing the shoulder in orientations requiring special stabilization, especially while slowly moving through the canopy.

It has long been thought that hominoids are best defined by a common set of morpho-functional traits related to the trunk and upper limb, in which the scapula is characterized by being located on the back of the ribcage, while the glenohumeral joint would be adapted to allow extensive abduction (Keith, 1923; Rose, 1997; Larson, 1998). It has been suggested that these shared characteristics are related to forelimb-suspensory locomotion or brachiation. This idea has led us to consider hominoids as being relatively homogenous postcranially (Ward, 1997), despite evidence indicating that there is more variability than initially believed (Larson, 1998). For instance, locomotor ecology and recent analyses of the available fossil evidence indicate that suspensory locomotion may have been acquired independently by several hominoid lineages. In fact, it has been argued that Miocene apes characteristically lack many of the traits associated with suspensory behaviors that are present in their crown descendants (e.g., *Sivapithecus* and *Pongo*) (Begun and Kivell, 2011). The possible physical attributes of the last common ancestor of all hominoids have been discussed for a long time (Pilbeam, 2002). It has been traditionally thought that the majority of the postcranial resemblances of the crown hominoids correspond to shared-derived features (Schultz, 1930; Larson, 1998), however based on Miocene hominoid postcranial discoveries, this perspective has been recently re-examined (Begun and Kordos, 1997; Larson, 1998). These new fossils exhibit morphologies that differ with what would have been typically expected, thus raising the possibility that some of the extant ape postcranial similarities could be homoplasies (Begun, 1993). Furthermore, the inferences regarding Miocene hominoid positional behavior have shown that most of the fossil taxa seems to differ from the extant apes in that they seem to have been pronograde arboreal quadrupeds, although some exceptions have been proposed as well (Rose, 1997; Ward, 1997; Moyà-Solà et al., 2009). Although this research did not try to address this issue directly, the results show there is no generic and homogenous scapular morphology, but it noticeably varies in the different analyzed taxa. Hominoid scapular shape variation seems to be firstly distinguishing between "broad" versus "slender" scapulae, while secondly between arboreal and non-primarily arboreal hominoids. This morphological arrangement can be useful when discussing if the arboreal specializations observed in some of this species are in fact symplesiomorphies, as usually interpreted, or on the contrary represent evolutionary adaptations to novel environments. Hence it is important to consider this information when testing evolutionary models that explain the appearance of suspensory features gradually accreting in time (Moyà-Solà et al., 2004) or evolving as an integrated array (Pilbeam, 1996).

A limitation of the present study is that in reality shoulder soft tissues would mostly cope with strain and stress experienced by the shoulder (especially during the suspension scenario) but due to simplicity reasons, they were not modeled. In fact one of the main limitations of the proposed loading scenarios is that none of the muscular, ligamentous, capsular, fascia, or tendinous elements were considered, due to the absence of standardized data or because it was not possible to find information about their properties for all the analyzed species. Even though this is an unrealistic assumption, the objective of the present study was mostly comparative. Another limitation is that only relatively few stress values were analyzed (just 101 values in one slice of the models), which merely represents a localized part of the scapular biomechanical performance. Even though it was sufficient to carry out the presented analyses, following studies should include stress values more widely distributed on the scapula.

The present study has showed that the analysis of form and function using GM and FEA was able to cast some light regarding the functional and phylogenetic contributions in hominoid scapular morphology. Future studies should generate an integrative approach to analyze both shape and biomechanical data using more realistic loading scenarios derived from both observational and simulation data (e.g., multibody dynamics).

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